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LETTER

Climate change would lead to a sharp acceleration of Central African forests dynamics by the end of the century

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Keywords: tropical rainforest, climate change, CORDEX-Africa, M'Baïki experimental site, ecological guilds, mixture of matrix models, variable selection

Supplementary material for this article is available online

Abstract

Impacts of climate change on the future dynamics of Central African forests are still largely unknown, despite the acuteness of the expected climate changes and the extent of these forests. The high diversity of species and the potentially equivalent diversity of responses to climate modifications are major difficulties encountered when using predictive models to evaluate these impacts. In this study, we applied a mixture of inhomogeneous matrix models to a long-term experimental site located in M'Baïki forests, in the Central African Republic. This model allows the clustering of tree species into processes-based groups while simultaneously selecting explanatory climate and stand variables at the group-level. Using downscaled outputs of 10 general circulation models (GCM), we projected the future forest dynamics up to the end of the century, under constant climate and Representative Concentration Pathways 4.5 and 8.5. Through comparative analyses across GCM versions, we identified tree species meta-groups, which are more adapted than ecological guilds to describe the diversity of tree species dynamics and their responses to climate change. Projections under constant climate were consistent with a forest ageing phenomenon, with a slowdown in tree growth and a reduction of the relative abundance of short-lived pioneers. Projections under climate change showed a general increase in growth, mortality and recruitment. This acceleration in forest dynamics led to a strong natural thinning effect, with different magnitudes across species. These differences caused a compositional shift in favour of long-lived pioneers, at the detriment of shade-bearers. Consistent with other field studies and projections, our results show the importance of elucidating the diversity of tree species responses when considering the general sensitivity of Central African forests dynamics to climate change.

1. Introduction

Among the multiple increasing anthropogenic factors that will affect tropical forests (Lewis *et al* 2015), climate change appears to be both the most global and inevitable one. Through the alteration of temperature and rainfall, climate change could alter the structure, composition and functioning of tropical forests. Knowing the climate response of these forests is a major challenge in view of their crucial role as large-scale carbon stocks and sinks to contain global warming well below 2 °C (Griscom *et al* 2017, Rogelj *et al* 2018).

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Existing studies have largely focused on Amazonia. Simulations of climate change impact have suggested that Amazonian forests could rapidly decline as a result of enhanced droughts and accelerated temperature increase: the Amazonian die-back (Cox *et al* 2004). Inversely, some models have projected a greening-up of Amazon forests with an overall gain in productivity as the fertilisation effect of increasing CO_2 concentration overcompensates for the losses due to changes in temperature and precipitation (Huntingford *et al* 2013). Considering Amazon forests as a carbon sink may however be excessively optimistic and is still being debated (Lewis *et al* 2015).

As the second largest continuously forested area in the world, Central Africa is a key region for both climate change mitigation and adaptation (Niang *et al* 2014). Its importance for mitigation is largely recognised, with forests sheltering 80% of the above-ground African carbon stock (Mayaux *et al* 2013). In this region, depending on the climate scenarios, temperature is projected to increase in a range between 2 and 4 °C above the baseline observed in the second half of the 20th century reference (Aloysius *et al* 2016). Compared to temperature projections, precipitation projections from general circulation models (GCM) or from regional circulation models (RCM) are more heterogeneous, partly because of the difficulty in resolving climate mechanisms driving the variability of precipitation across Central Africa (Pokam Mba *et al* 2018). Changes in projected precipitation range from −9% to +27% (Aloysius *et al* 2016). Continental lands are projected to endure an intensification of dry seasons (Malhi *et al* 2013), a trend already widely observed for several decades (Zhou *et al* 2014).

The response of Central African forests to climate change has remained largely understudied until recently (Sonwa *et al* 2013), partly due to the lack of regional climate information (Lennard *et al* 2018). Tree species composition is strongly correlated with rainfall and temperature gradients (Fayolle *et al* 2014). The global study of Zelazowski *et al* (2011) on the role of climate in the distribution of humid tropical forests and the first regional impact assessment of climate change on the Congo Basin by Ludwig *et al* (2013) concluded that, in contrast to Amazonia, a die-back in Central African forests would be unlikely.

Relationships between climate variables and forest dynamic processes, i.e. growth, mortality and recruitment, are complex (Swann *et al* 2016). They are widely variable from one species to another resulting in species uniqueness in their possible response to climate change (Uriarte *et al* 2018). The same changes in climate could be beneficial to some species but detrimental to others, leading to shifts in floristic composition.

Tropical tree species responses to climate can be approximated through their shade-tolerance, generally by distinguishing ecological guilds (Hawthorne 1995) such as pioneers (P), non-pioneer light-demanders (NPLD) and shade-bearers (SB). In the Central African Republic (CAR), Ouédraogo *et al* (2013) showed that slow-growing SB species were the least sensitive to drought. On the contrary, in Ghana, drought might lead to a shift from SB species to dry-adapted P and NPLD species (Fauset *et al* 2012).

From a modelling perspective, tree species grouping, and more generally, plant functional classification (Lavorel *et al* 2007) is a tool for simplifying floristic complexity. There are various methods for grouping species, including groups based on the subjective ecological knowledge of species, such as widely-used Hawthorne (1995)'s guilds, or groups based on species dynamic processes, namely growth, mortality and recruitment (Gourlet-Fleury *et al* 2005). While subjective ecological groups facilitate the ecological interpretation of results, when it comes to simulating forest dynamics, it is better to build groups based on their own processes in order to improve the estimation of dynamics parameters and the projection performances (Mortier *et al* 2013, Picard *et al* 2010).

In this study, we aimed at disentangling the long-term effects of different climate variables on the structure and dynamics of a tropical rainforest in Central Africa. We hypothesised that climate change will have differential impacts on species dynamics with varying responses driven by different climate and structure variables within and across ecological guilds. We used a modelling approach based on Mortier *et al* (2015)'s mixture of inhomogeneous matrix models (MIMM), a methodology particularly well adapted to simulate the dynamic behaviours of species-rich ecosystems. We applied it to forest inventory data from a unique 30-year-long experiment established at M'Baïki, in CAR. To integrate the variability of climate projections, we produced 10 different versions of MIMM, one for each GCM. After comparing observed and simulated forest stands, we examined the impact of climate change on forest dynamics, in terms of both structure and composition, over the 21st century.

2. Material and methods

2.1. Data

2.1.1. Forest inventory data

Annual forest inventories have been performed since 1982 at the M'Baïki experimental site (figure S1 available online at stacks.iop.org/ERL/14/044002/mmedia), established in CAR (3° 54′N, 17°56′E). The vegetation is a Guineo-Congolian semi-deciduous moist forest, with canopy dominated by *Cannabacae*, *Myristicacae* and *Meliacae* families (Boulvert 1986). Ten permanent sample plots, four ha each, were established in two neighbouring forest reserves. Between 1982 and 2012, all trees $\geqslant$10 cm diameter at breast height (DBH) have been monitored. The floristic description of the trees is complete since 1992. Three disturbance treatments were implemented: three plots were left as controls, seven plots were selectively logged

of which four were subsequently thinned. Selective logging occurred between 1984 and 1985 and consisted of harvesting commercial trees with DBH $\geqslant$ 80 cm. Thinning occurred two years after logging and consisted in poison girdling all non commercial trees with DBH $\geqslant$ 50 cm and cutting all lianas. A complete description of the experimental site can be found in Gourlet-Fleury *et al* (2013).

2.1.2. Climate data

To predict the climate at M'Baïki over the next century, we used outputs of regional climate simulations over 1992–2100 conducted over the Coordinated Regional Climate Downscaling Experiment (CORDEX)-Africa domain at a resolution of ≈50 km (0.44° × 0.44°). These climate predictions are considered to be a good compromise between model performances and computational limits (Panitz *et al* 2014). CORDEX is a standardised framework in which GCM projections are dynamically downscaled by RCM over selected continent-scale regions (Jones *et al* 2011), including Africa (Hewitson *et al* 2012).

We used 10 GCM outputs (table S1), downscaled by the Rossby Centre regional atmospheric model (Samuelsson *et al* 2011). For each GCM, we used three sets of climate projections: the historical runs over the period 1992–2005 extended over 2006–2099, which we refer to as baseline scenario under constant climate; and the projected runs under two Representative Concentration Pathways (RCP), RCP 4.5 and RCP 8.5 (Moss *et al* 2010), over the period 2006–2100. The baseline scenario allowed, by comparison with the other two scenarios, the identification of forest dynamics that would or not be affected by climate change.

2.2. Forest dynamics modelling methodology

We used the MIMM methodology (Mortier *et al* 2015) to model the forest dynamics based on each of the 10 GCM used. MIMM is a statistical correlative model that identifies differential growth, mortality and recruitment processes, and selects their associated subsets of explanatory variables. It combines ideas of mixture models, generalised linear models (GLM), variable selection and matrix models. The MIMM method consists of two steps: (i) for each dynamic process, penalised finite mixtures of GLM are used to classify species into groups, select the best explanatory variables, and estimate the model parameters; (ii) a Usher (1966, 1969) matrix model is then calibrated for each non-empty identified group and used to project forest dynamics. Further details are provided in the supplementary section S1.3.

2.3. Simulation protocol

2.3.1. Fitting MIMM on GCM versions for M'Baïki

We used data collected on all the M'Baïki plots, regardless of the disturbance treatment applied, and data from CORDEX-Africa historical runs, to fit MIMM to the various GCM and to define the composition and the parameters associated to species groups, over the 1992–2005 period. This enabled us to quantify the dynamic processes over a large range of stand conditions, using ≈120 000 diameter increments measures, 3600 death and 6100 recruitment events.

Table 1. List of explanatory climate and structure variables used in this study. Climate variables are those kept using a VIF $<$ 5 criterion.

Label	Long name
Climate variables	
clt	Total cloud fraction
mrr	Total runoff
sfw	Daily maximum near-surface wind speed
snd	Duration of sunshine
tas	Near-surface air temperature
uas	Eastward near-surface wind
vas	Northward near-surface wind
Structure variables	
bsl	Stand basal area
dmt	Diameter at breast height
dns	Stand density
ldm	Log-diameter at breast height

We processed the climate data after extracting the 30 arc s (≈1 km^2) pixel corresponding to the M'Baïki site from raster maps of climate variables. For this pixel we averaged, on an annual basis, monthly time series of 13 climate variables. We excluded six highly correlated variables, using a variance inflation factor (VIF) threshold of 5 (Dormann *et al* 2013). We thus kept seven climate variables to calibrate MIMM (table 1). Climate variables were complemented by four structure variables calculated from the M'Baïki forest inventories and directly linked to the development of trees and forest stands: DBH (in cm) and its logarithmic transformation, log-DBH, to deal with the nonlinear association between DBH and the growth and mortality processes; stand density (stems per hectare, in ha^{-1}) and stand basal area (in m^2 ha^{-1}) to quantify the tree competition effect on growth, mortality and recruitment processes.

We assessed the observed and projected stand structures based on four output variables: stand density (ha^{-1}), stand basal area (m^2 ha^{-1}), quadratic diameter (cm) and carbon biomass ($t_{eq}CO_2$ ha^{-1}). We calculated the first three variables directly from the MIMM outputs at each time step while we estimated carbon biomass by combining the MIMM outputs with a pantropical allometric equation (Chave *et al* 2014) with the conversion rate from biomass to carbon set to 0.47 (Eggleston *et al* 2006, table 4.3). We took species-specific wood densities from the database of Zanne *et al* (2009). When there was no match at the species level, we used the average value at the genus level. When no value was available in the database, we used the default 0.60 g cm^{-3} recommended by Henry *et al* (2010, p. 1383) for tropical African woods.

2.3.2. Simulation of forest dynamics

For each of the 10 GCM, three simulation analyses were conducted. The first analysis, for calibration, aimed at comparing simulated and observed stands at M'Baïki. It involved running simulations from 1992 to 2005. The two other analyses, for validation and projection, started in 2006, when historical runs of GCM were no longer available. The three different climate scenarios presented in section 2.1.2 were used for validation and projection. The validation analysis ended in 2012, when the last forest inventories at M'Baïki were available. This was done to compare projected forest stands to observed stands under different climate scenarios. The projection analysis ended in 2099 and aimed to simulate the impact of climate change over the 21st century, starting with the average abundance of the control plots at M'Baïki.

2.3.3. Atmospheric CO_2 concentration as an explanatory variable

While recent studies show that atmospheric CO_2 concentration varies both spatially and seasonally across the world (Zhang *et al* 2013), this variable was not available in CORDEX-Africa. In an attempt to consider CO_2, we averaged GCM projections of atmospheric CO_2 concentration under the Coupled Modeal Intercompariosn Project Phase 5 (CMIP5) (Taylor *et al* 2012) and included this average as a covariate in the 10 GCM versions. MIMM was fitted with and without this variable to assess the relevance of including CO_2 concentration as a covariate.

Although the calibration and validation procedures could be successfully completed, the simulations over the projection period systematically failed to converge when including CO_2. Forest dynamics reached unrealistic levels, with infinite values in stand characteristics and processes. This failure was due to the perfect correlation of the annual average atmospheric CO_2 concentration with time. Thus, CO_2 effect was confounded with linear temporal trend, a situation that prevents any valid projection. In the following, only results obtained without CO_2 concentration are presented.

2.3.4. Summarising MIMM outputs

Because the number of species combined to the 10 GCM versions led to an impractical number of information, results were summarised by re-aggregating MIMM's outputs according to the two following approaches. The first, exogenous to MIMM, is based on ecological guilds, the second, endogenous to MIMM, is based on the similarities of species groupings between GCM versions. For the latter, we used hierarchical clustering to define new meta-groups. The number of meta-groups was estimated using the gap statistics (Kaufman and Rousseeuw 2005). In comparison to guilds, meta-groups are more consistent with the information from the data as they follow the same logic of species grouping based solely on the similarity of their dynamic processes (Picard *et al* 2010). Further details are provided in the supplementary section S2.1. The contributions of variables to projected changes in dynamic processes were quantified using weighted averages across GCM versions of the correlations between the linear predictor associated to a variable and the projected values (see supplementary section S1.3).

3. Results

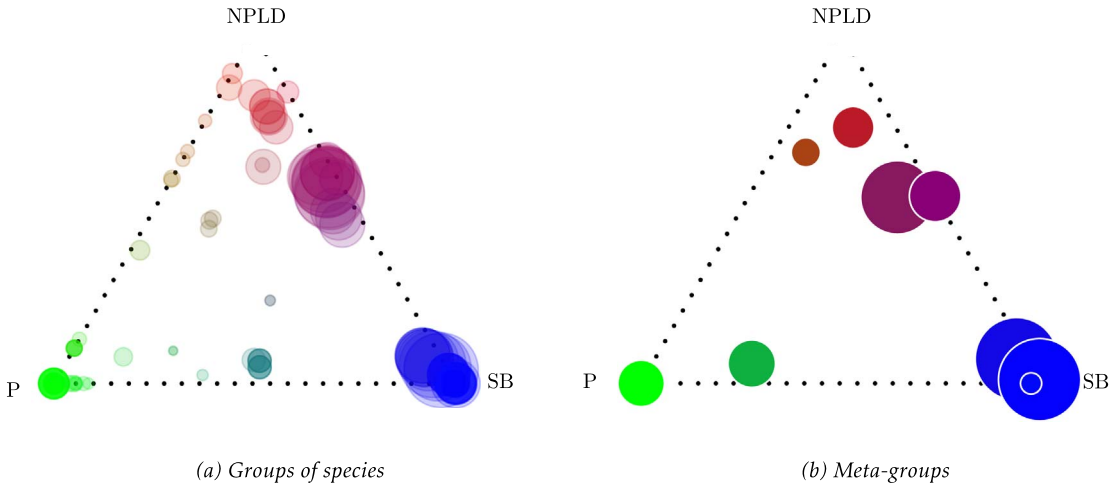
3.1. Species groups and explanatory variables

Among the 10 different GCM versions used for applying MIMM to the M'Baïki data, the number of groups identified ranged between 5 and 8 for the growth process, and 2 and 4 for the recruitment process. For the mortality process, all versions agreed on 3 groups. Allocating species across growth, mortality and recruitment groups resulted in 11 to 17 non-empty growth-mortality-recruitment combined groups. In these groups, depending on the GCM version, the number of species was variable with the largest groups containing between 35 and 67 species, and the average group between 12.2 and 18.9 species. The number of species groups obtained by model fitting and the species composition of these groups showed similarities and differences across GCM versions (figure 1(a)). The cluster allocation of species and the parameter estimates are provided for each GCM version in supplementary section S3.

To refine comparisons, we disaggregated model projections from the group to the species level, and then re-aggregated them at the guild level and at the meta-group level. The differences between groups, guilds and meta-groups are illustrated in figure 1 and detailed in figure S2. Some species groups, especially some P-dominated or SB-dominated groups were quite well discriminated on the basis of their guild composition. The majority of groups mixed species from two or all three guilds. In particular, no group was exclusively composed of NPLD.

Nine meta-groups were identified with a hierarchical cluster analysis and gap statistics (figure S2 and table 2). Meta-groups 1, 5 and 6 were highly dominated by SB. Meta-groups 2 and 3 were dominated by NPLD, meta-group 4 by long-lived P and meta-group 9 by short-lived P. The two remaining meta-groups 7 and 8 are dominated by NPLD and SB, in similar proportions.

The climate and structure variables selected to be associated with the dynamic processes varied across the GCM versions, guilds and meta-groups (tables S2 and S3). At the guild level, all structure variables were generally selected to explain dynamic processes with the exception of stand density for growth. All climate variables are generally selected to explain growth, but were not systematically selected for mortality and recruitment. The selection of the variables varied within guilds, reflecting the heterogeneity of specific responses within guilds. For example, climate variables had a large variability in their selection for mortality among P. At



(a) Groups of species *(b) Meta-groups*

Figure 1. Overlapping projection of groups of species for each GCM version (subfigure 1(a)) and of meta-groups (subfigure 1(b)). For each point, the size is proportional to the number of trees clustered in the group or meta-group, and the colour and stand position correspond to the guild composition of these trees: the more trees from P (respectively, NPLD and SB) in the group or in the meta-group, the closer the point to the P (respectively, NPLD and SB) summit of the simplex with green (respectively, red and blue).

Table 2. Ecological description of the meta-groups. From left to right, columns indicate the most abundant species inside each meta-group, the number of trees, the number of species, the maximum DBH (in cm), the diameter increment (in cm yr^{-1}) and the proportions , expressed in reference to the number of trees, of each regeneration guild (in %).

						Guild composition (%)		
Meta-group	Dominating species	Number of trees	Number of species	Maximum DBH (cm)	Mean growth (cm yr^{-1})	P	NPLD	SB
1	*Garcinia punctata*	6978	42	37.5	0.11	0.4	1.0	98.6
2	*Entandrophragma cylindricum*	880	14	112.7	0.49	25.9	66.2	7.9
3	*Petersianthus macrocarpus*	1810	18	106.9	0.44	10.6	73.3	16.1
4	*Bosqueia angolensis*	2321	26	96.8	0.75	69.6	5.7	24.7
5	*Strombosia grandifolia*	461	5	70.8	0.25	3.0	0.0	97.0
6	*Staudtia kamerunensis*	7042	43	60.6	0.17	3.1	7.0	89.9
7	*Celtis zenkeri*	5544	42	77.2	0.31	9.6	53.3	37.1
8	*Pycnanthus angolensis*	2748	14	103.4	0.31	0.0	53.7	46.3
9	*Musanga cecropioides*	2233	4	100.5	1.27	99.9	0.0	0.1

the meta-group level, the frequency of selection for the variables had narrower range, indicating less heterogeneity of species responses within meta-groups than within guilds, the best example being meta-group 5. However, contrasts in terms of variable selection can be observed between meta-groups, for example on growth (stand density is less selected in meta-groups 1 and 2) and on recruitment (climate variables are less selected in meta-groups 2 and 3).

3.2. Model validation

Over the calibration period (1992–2005), no significant difference was found between simulations and observations on forest structure and dynamics, across all disturbance treatments except for a slight underestimation of recruitment in logged plots (figure 2). Interestingly, MIMM was able to capture the effects of disturbance treatments, with a clear impact of logging and/or thinning on forest dynamics.

Over the validation period (2006–2012), simulated forest structure and dynamics remained close to the observed data for all climate change scenarios and disturbance treatments, except a slight overestimation of growth and recruitment in treated plots. In particular, some trends such as the decrease of stand density and recruitment, as well as the increase of basal area, quadratic diameter and carbon biomass were well captured by MIMM.

3.3. Baseline scenario

Under the baseline scenario, with constant climate conditions over the projection period 2006–2099, the forest dynamics and structure projected in 2099 differed from those observed in 2005 (figure 3). The

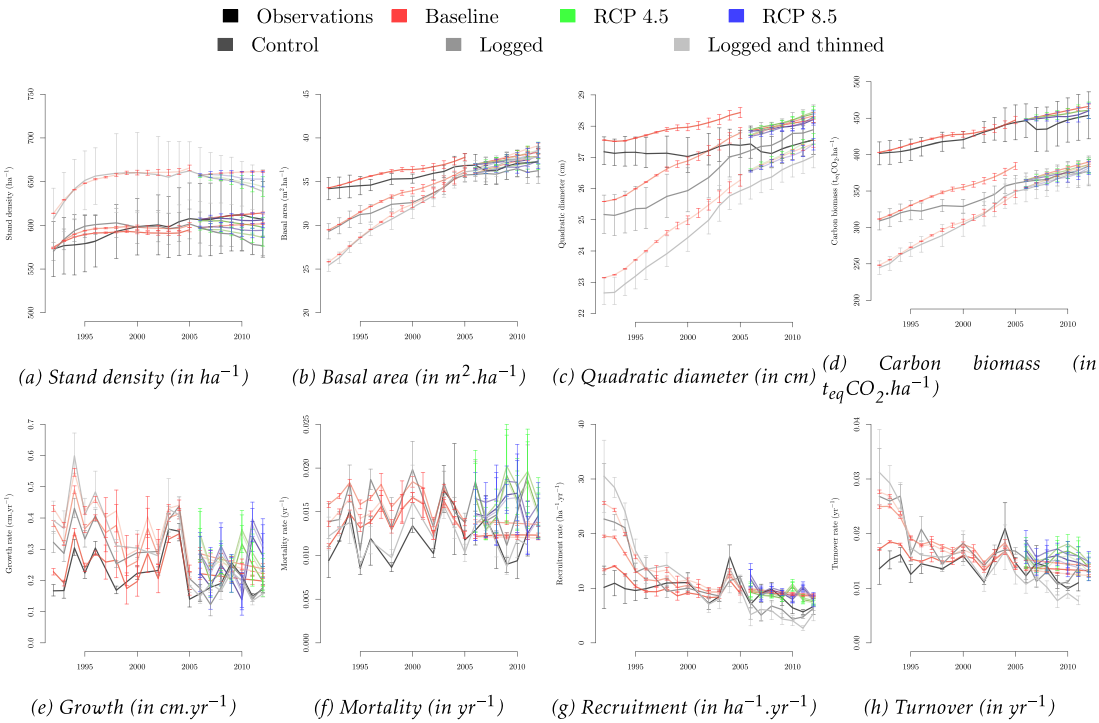


Figure 2. Change over time of the mean observed and simulated output variables describing forest structure for each disturbance treatment under different climate scenarios: stand density (in ha^{-1}, subfigure 2(a)), stand basal area (in m^2 ha^{-1}, subfigure 2(b)), quadratic diameter (in cm, subfigure 2(c)), above-ground carbon biomass (in $t_{eq}CO_2$ ha^{-1}, subfigure 2(d)), growth (in cm yr^{-1}, subfigure 2(e)), mortality (in yr^{-1}, subfigure 2(f)), recruitment (in ha^{-1} yr^{-1}, subfigure 2(g)) and turnover (in yr^{-1}, subfigure 2(h)). For both observation and simulations, the three treatments at M'Baïki are plotted separately. Over the calibration period (1992–2005), simulations start from average treatment-specific forest stands in 1992 and integrate historical runs as climate series until 2005. Later on, simulations are run under three climate scenarios: the constant average climate in historical runs between 1992 and 2005, RCP 4.5 and RCP 8.5. Uncertainty bars around observations correspond to the variability between the M'Baïki sample plots. Uncertainty bars around predictions correspond to the variability between the different GCM versions.

projected stand basal area, quadratic diameter, and carbon biomass in 2099 were significantly higher than the 2005 levels (p-values $<10^{-3}$), while the projected stand density did not differ from the observed one in 2005 (p-values >0.05). Regarding dynamics, the projected mortality and recruitment in 2099 did not differ from the ones observed in 2005 (p-values >0.05), while the projected growth in 2099 was significantly lower than the 2005 level (p-values <0.01). These results showed evidence of a forest ageing phenomenon with fewer but larger trees and reflected that natural forests in M'Baïki are not at equilibrium (Gourlet-Fleury *et al* 2013).

At the guild level, some differences were also found between projections in 2099 and the observed values in 2005. Projected quadratic diameter and carbon biomass of NPLD and SB species in 2099 were all significantly higher than the observed values in 2005 (p-values $<10^{-3}$). The basal area of SB species was also significantly higher than the one observed in 2005 (p-value $<10^{-3}$). Conversely, the basal area and quadratic diameter of P species projected in 2099 were significantly lower than the observed values in 2005 (p-values <0.05). Moreover, projected growth in 2099 was significantly lower for all guilds than the levels observed in 2005 (p-values <0.01). Projected mortality in 2099 was significantly higher than observations for NPLD species in 2005 (p-value $<10^{-3}$). We found no difference between projected and observed recruitment for all guilds.

At the meta-groups level, the composition remained almost unchanged between observations in 2005 and projections in 2099, and we found no significant difference in stand density (figure 4). Projected quadratic diameters in 2099 were significantly higher compared to 2005 observed values for all meta-groups except 4, 5 and 9 (significantly lower for meta-group 9). Growth was projected lower in 2099 compared to the observed values in 2005 except for meta-groups 2 and 8. Projected mortality in 2099 was significantly higher than the observed values in 2005 for meta-groups 2, 3 and 9. Recruitment was projected significantly lower for meta-group 1 and significantly higher for meta-groups 5 and 8 in 2099 compared to the 2005 observed levels. These results were also consistent with forest ageing, with a general decline in growth, and a decreased abundance of pioneers in favour of shade-tolerant species.

3.4. Impacts of climate change on forest structure and dynamics

RCP 4.5 and 8.5 scenarios projected a strong impact of climate change on the structure and the dynamics of forest stands, compared to the projections under the

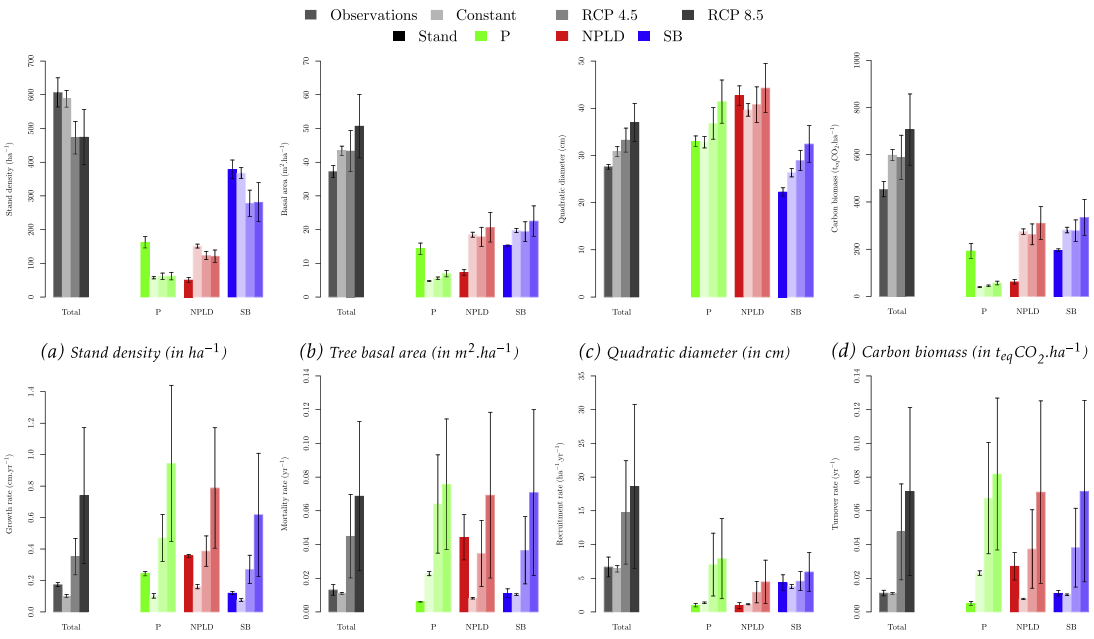


Figure 3. Average values and standard errors of output variables describing the structure and dynamics of observed and projected forest stands, at the stand and at the guild levels. Structure variables are stand density (in ha^{-1}, subfigure 3(a)), tree basal area (in m^2 ha^{-1}, subfigure 3(b)), quadratic diameter (in cm, subfigure 3(c)) and above-ground carbon biomass (in $t_{eq}CO_2$ ha^{-1}, subfigure 3(d)). Dynamics processes are growth (in cm yr^{-1}, subfigure 3(e)), mortality (in yr^{-1}, subfigure 3(f)) and recruitment (in ha^{-1} yr^{-1}, subfigure 3(g)) while turnover rate (in yr^{-1}, subfigure 3(h)) is also given. For each variable or process, values are indicated at the whole-stand level (first set, in grey) from left to right, and at the guild level (green, red, blue for P, NPLD and SB, respectively). Each set of barplot is composed of four bars, with more or less saturated colour, representing from left to right: M'Baïki control plot observations between 1992 and 2005 (first bar, the most saturated), projected stands under constant climate (second bar, the least saturated), projected states under RCP 4.5 and RCP 8.5 in 2099 (3rd and 4th bars, respectively, with lower and upper intermediary saturations).

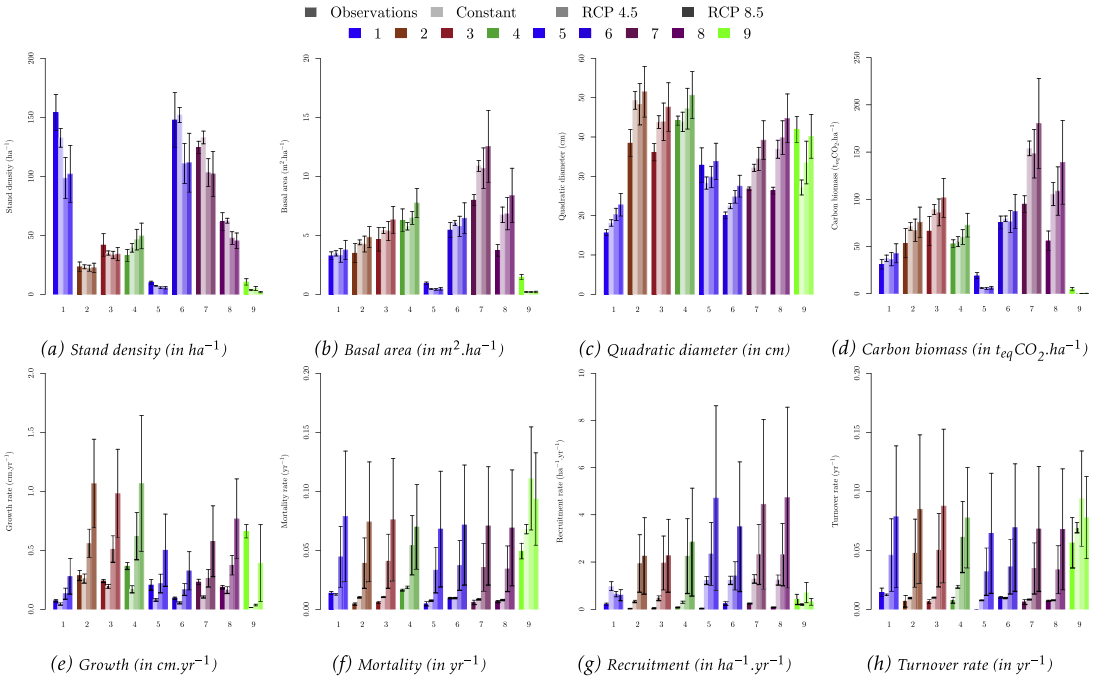
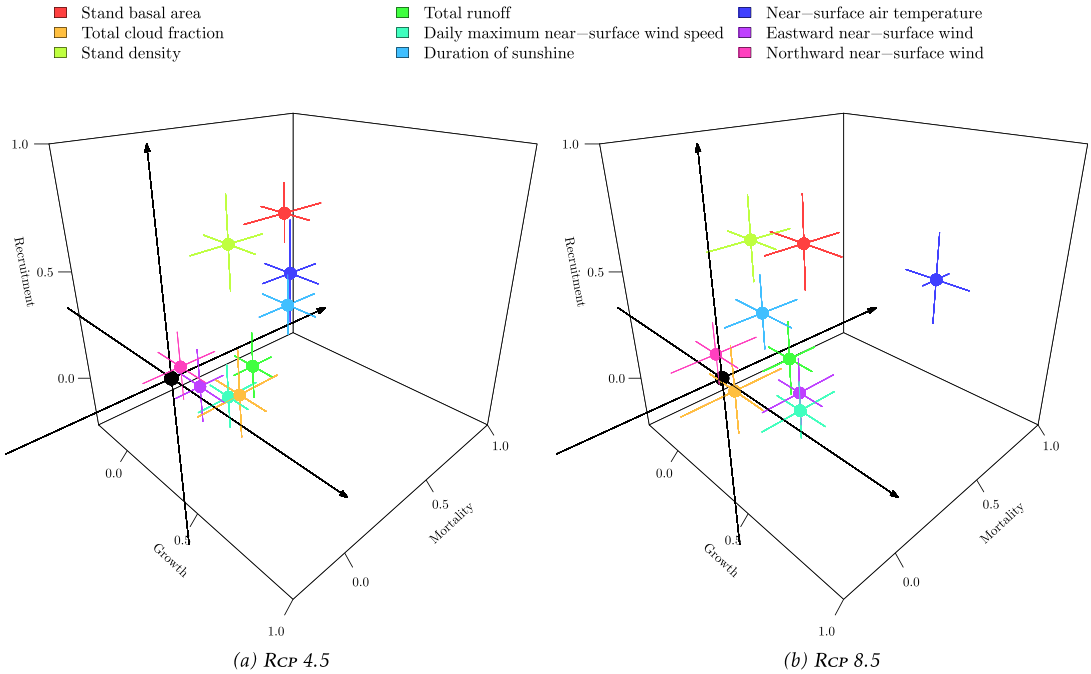


Figure 4. Same as figure 3, but for meta-groups.



(a) RCP 4.5 (b) RCP 8.5

Figure 5. Trivariate representation of the contribution of explanatory variables, except tree variables DBH and *log*-DBH, to the change of growth, mortality and recruitment over time, for RCP 4.5 and 8.5. Segments represent the variability (standard errors) across the different GCM versions. A value of 1 means that the projected contribution of the variable is perfectly correlated to the projection of the dynamic process based on all the explanatory variables while a null contribution means that the variable does not contribute to the projection of the dynamic process.

baseline scenario (figure 3). The same trend, namely an acceleration of forest dynamics due to an enhancement of growth, recruitment and mortality processes, was observed in the great majority of the simulations under all scenarios, but with a higher variability for RCP 8.5 than for RCP 4.5.

Growth increased by a factor of 3.4 ± 1 under RCP 4.5 and a factor of 6.8 ± 4 under RCP 8.5 compared to the baseline scenario. Mortality was multiplied by 3.7 ± 2 under RCP 4.5 and 5.7 ± 3 under RCP 8.5, while recruitment, divided by stand density, was multiplied by 3.9 ± 2 under RCP 4.5 and 5.7 ± 4 under RCP 8.5. For the baseline scenario, the turnover (calculated as the average of mortality and recruitment rates) was found to equal 1.1 ± 0.05% while for the RCP 4.5 and 8.5, it equalled 4.7 ± 3% and 7.1 ± 5% respectively. Considering the contribution of each variable to each dynamic process (figure 5), projected changes of growth appear to be mainly driven by stand basal area and sunshine duration under RCP 4.5 and by temperature under RCP 8.5. Projected changes of recruitment appear to be mainly driven by stand basal area and stand density, while projected changes of mortality appear to be driven by temperature and, to a lesser extent, by total runoff.

Climate change significantly impacted the stand density as well as the structural characteristics of the forest: a thinning phenomenon was observed with stand density falling from 588 ± 25 ha^{-1} to 473 ± 48 ha^{-1} under RCP 4.5 and to 474 ± 81 ha^{-1} under RCP 8.5, paralleled with an increase of the quadratic diameter from 31 ± 1 cm to approximately 33 ± 3 cm under RCP 4.5 and 37 ± 4 cm under RCP 8.5.

The impacts of climate change differed from one guild to another. It was found to favour P over SB (no significant effect on NPLD). The proportion of SB fell from 62 ± 0.5% to 56 ± 4% under RCP 4.5 and to 55 ± 5% under RCP 8.5, while the proportion of P increased from 10 ± 0.4% to 16 ± 5% under RCP 4.5 and to 17 ± 5% under RCP 8.5. Meanwhile, the proportion of NPLD remained around 26%. P turnover rose from 2.3 ± 0.1% for the baseline scenario, to 6.8 ± 3% under RCP 4.5 and 8.2 ± 5% under RCP 8.5. NPLD and SB turnover shared the same pattern of increased turnover: from 0.78 ± 0.03% to 3.7 ± 2% and 7.1 ± 5% (NPLD species); from 1 ± 0.04% to 3.8 ± 2% and 7.2 ± 5% (SB species). Dynamic processes appeared to be driven by the same climate variables at the guild-level than at the stand-level (figure S3, same plotting method as in figure 5). NPLD and SB dynamic processes appeared to be driven by a larger number of climate variables than P dynamic processes, suggesting a higher sensitivity of SB and NPLD to climate variables.

Forest dynamics acceleration, albeit with much more variability under RCP 8.5 compared to RCP 4.5, was a general trend projected for all processes and all meta-groups (figure 4), with the sole exception of recruitment for meta-group 1 that decreased with time. The magnitude of increase varied greatly from one meta-group to the other leading to changes in the

composition of the forest. The natural thinning effect projected at the whole-stand level mainly affected the most abundant meta-groups in the control stands, dominated by SB—the relative proportion of meta-groups 1, 6 and 7 fell from 22 ± 7.1%, 26 ± 8.2%, 23 ± 7.2% in the control stands to 19 ± 5.9%, 21 ± 6.6%, 20 ± 6.5% under RCP 8.5—and favoured meta-group 4 dominated by long-lived P, whose relative proportion doubled from 7 ± 2.1% to 14 ± 4.6%, and meta-groups dominated by NPLD—the relative proportion of meta-groups 2 and 3 rose from 4 ± 1.2% and 6 ± 1.9% to 6 ± 1.8% and 9 ± 2.7%.

The climate drivers of dynamic processes were variable across meta-groups (figure S4 and S5, same plotting method as in figure 5). Under RCP 4.5, growth was driven by duration of sunshine for all meta-groups except 9. Under RCP 8.5, growth was driven by temperature for all SB- and NPLD-dominated meta-groups, but no driver was found for the growth of P-dominated meta-groups 4 and 9. For mortality, the temperature was the most relevant variable for all meta-groups and scenarios. Under RCP 4.5, recruitment was driven by duration of sunshine for all meta-groups, by temperature for SB-dominated groups and also by total runoff for meta-group 9. Under RCP 8.5, temperature was found relevant for the recruitment of P- and SB-dominated meta-groups.

4. Discussion

We used MIMM, a method allowing the simultaneous clustering of species into groups according to dynamic processes (growth, mortality and recruitment) and the identification of group-specific explanatory climate and structure variables. We projected the dynamics of M'Baïki forest stands over the 21st century under a constant climate scenario and under two scenarios of climate change, RCP 4.5 and 8.5. We showed that climate change would lead to a sharp acceleration of forest dynamics, with an increase of growth, mortality and recruitment, leading to changes in forest structure and composition, namely a natural thinning effect with fewer but larger trees, and an increase in the relative proportion of pioneers at the detriment of shade-bearers.

4.1. Climate change would accelerate the dynamics of tropical forests

The simultaneous increase of growth, mortality and recruitment, as well as basal area and aboveground biomass, is consistent with historical observations in the M'Baïki forests (Gourlet-Fleury *et al* 2013) and has already been well documented at a pantropical scale (Malhi *et al* 2014). Our projections are also consistent with projections from pantropical studies (Lewis *et al* 2015) and Central African studies (Ludwig *et al* 2013).

Our simulations projected a slight increase of carbon biomass. This result is also consistent with previous projections in tropical forests which suggested that climate change induces a shift from low-biomass forests to high-biomass forests (Kim *et al* 2017). The increase of carbon biomass projected in our baseline scenario, without climate change, is consistent with observations of forest ageing. It can be explained by a recovery from past human-induced disturbance (Morin-Rivat *et al* 2014).

4.2. Climate change would affect forest composition by favouring long-lived pioneers

The magnitude of the projected changes in dynamics varies from one group of species to another and this differential response leads to a change in the relative species composition of forest stands, resulting in an increase of the relative proportion of pioneers, at the detriment of shade-bearers. In particular, we projected a rise of long-lived pioneers (meta-group 4) at the detriment of shade-bearers (meta-groups 1, 6 and 7). Compared to shade-bearers, pioneers have higher light requirements, faster growth and are more disturbance-adapted. Some studies have already reported shifts in tree composition favouring fast-growing species over slow-growing ones (Wright 2005) and have hypothesised a response to climate change. The expected higher dominance of pioneers may also raise questions about the future capacity of Central African forests to cope with droughts. Indeed, although pioneers are mostly deciduous and therefore well adapted to seasonal drought, the increase in their dominance may have a negative effect on the global ecosystem resistance to water stress because pioneers that allocate their resources to fast growth are less resistant to water stress (Aubry-Kientz *et al* 2015).

4.3. Climate drivers and particularly temperature have significant effects on the dynamic processes

Projected growth appeared to be mainly driven by stand basal area and sunshine duration under RCP 4.5 and by temperature under RCP 8.5. Projected recruitment of forests is found to be mainly driven by stand basal area and stand density, while projected mortality appeared to be driven by temperature and, to a lesser extent, by total runoff. These results highlight the sensitivity of forests to climate (Anderson-Teixeira *et al* 2013) with sunshine duration (a proxy of the energy reaching the forest system), water availability and temperature as the main drivers. The positive influence of sunshine duration on growth has already been stressed by Dong *et al* (2012). The influence of total runoff as a proxy for water availability, is in line with other studies showing the importance of drought in tree mortality (Phillips *et al* 2010, eg).

The positive correlation between mortality and temperature is consistent with observations from field studies (Clark *et al* 2010). However the positive

correlation between growth and temperature contradicts most of the results from the Amazon (Aubry-Kientz *et al* 2015). The temperature-sensitivity of growth observed in Amazon forests may not be valid in African forests, as the latter are presumably more resilient to climate change than Amazon forests (Malhi *et al* 2014). This contradiction could also be resolved considering the nonlinearity of relationships between temperature and photosynthesis (Hüve *et al* 2011): tropical tree species may be near a high temperature threshold that, if exceeded, will greatly reduce growth (Doughty and Goulden 2008). Amazon forests would already have crossed this threshold whereas Central African forests may still be below it. In this case, our projections might not have captured this threshold effect.

4.4. Meta-groups sharpen differences in species response to climate change that are less evident with guilds

The elaboration of optimal species aggregation techniques for modelling the dynamics of species-rich ecosystems remains an active research area (Kazmierczak *et al* 2014). The comparison of several climate calibrations shows a great similarity in the way species are grouped, making it possible to identify meaningful ecological meta-groups. The identified meta-groups differ in many ways from Hawthorne (1995)'s guilds: species with different dynamic profiles can be distinguished within the same guild, notably among pioneers, while other species are grouped together although they are considered to belong to distinct guilds, notably SB and NPLD. Compared to exogenous guilds, our meta-groups have the advantage to be an endogenous result from the model and to reflect the species-specific dynamic responses to climate variables in a more accurate way than guilds. More generally, in the continuation of the work of Gourlet-Fleury *et al* (2005), Picard *et al* (2010) and Mortier *et al* (2015), our results show the value of using dynamics data-driven classifications rather than classifications based on ecological knowledge to simulate long-term forest dynamics.

To refine the grouping of species based on their response to climate change, further developments can be considered, for example through the ongoing CMIP6 (Eyring *et al* 2016) and advances in the use of extended matrix of GCM-RCM experiments (Wilcke and Bärring 2016), or through the incorporation of ecophysiological processes (Feng *et al* 2018), especially to deal with the effects of increased atmospheric CO_2. These would offer new opportunities to enhance the future projections of climate change and to improve the understanding of its impact on tropical forest dynamics (Malhi *et al* 2014).

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Authors' contribution

FC, FM, SGF and NP conceived the ideas and designed methodology. MT helped on methodological aspects and contributed to the results' discussion. GC supported authors on computational aspects. FaB, FiB and SGF collected and organised the data. DYO and BH contributed to the discussion of results. All authors contributed critically to the drafts and gave final approval for publication.

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